

THE STATUS OF THE CENTRAL AMERICAN
LEPTODACTYLID FROGS *ELEUTHERODACTYLUS*
MELANOSTICTUS (COPE) AND *ELEUTHERODACTYLUS*
PLATYRHYNCHUS (GÜNTHER)

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Abstract.—*Eleutherodactylus melanostictus*, a species unique to the genus in lower Central America in having dark transverse bars on the anterior, dorsal, and posterior surfaces of the thighs, is redefined. *E. platyrhynchus* is conspecific with *melanostictus*. In external and skeletal morphology the species seems allied to the *unistrigatus-cruentus* series. Jaw musculature (dfsq + e) allies this species to the *fitzingeri-rugulosus* series, whereas all known representatives of the *unistrigatus-cruentus* stock have a very distinctive set of jaw muscles (DFSQ_dAT + s). Karyologically the species has 2N = 22, N.F. = 36 and resembles several members of the *fitzingeri-rugulosus* series, especially *E. berkenbuschii* of eastern Mexico. Known members of the *unistrigatus-cruentus* series have 2N = 26, 32, 34; N.F. = 32, 36, 46. These differences make *E. melanostictus* the sole representative of a monotypic species group.

Among the numerous species of rain frogs, genus *Eleutherodactylus*, found in the cordilleras of Costa Rica and western Panama, is a series of populations distinctive from all others in having transverse dark bars on the anterior, dorsal, and posterior surface of the thighs. In life the contrasting light interspaces on the posterior thighs range from cream through yellow-green to orange, salmon, magenta, and scarlet to make these animals among the most conspicuous forms in the genus. Several names have been applied to the populations—including *Hylodes brocchi* Boulenger, 1882 (Günther, 1900), now known to be restricted to Guatemala (Savage, 1975); *Lithodytes melanostictus* Cope, 1875; and *Hylodes platyrhynchus* Günther, 1900 (Dunn, 1937; Taylor, 1952), each based on Costa Rican frogs.

Prior to 1960 these frogs were known from a few individuals from scattered localities. While the problem of the status of the various samples has been recognized for some years, it is only now that sufficient material has been accumulated to make a review of the populations possible.

Comparison of Populations

Frogs of the *melanostictus-platyrhynchus* population system are found along the slopes of the cordilleras of Costa Rica and western Panama, from

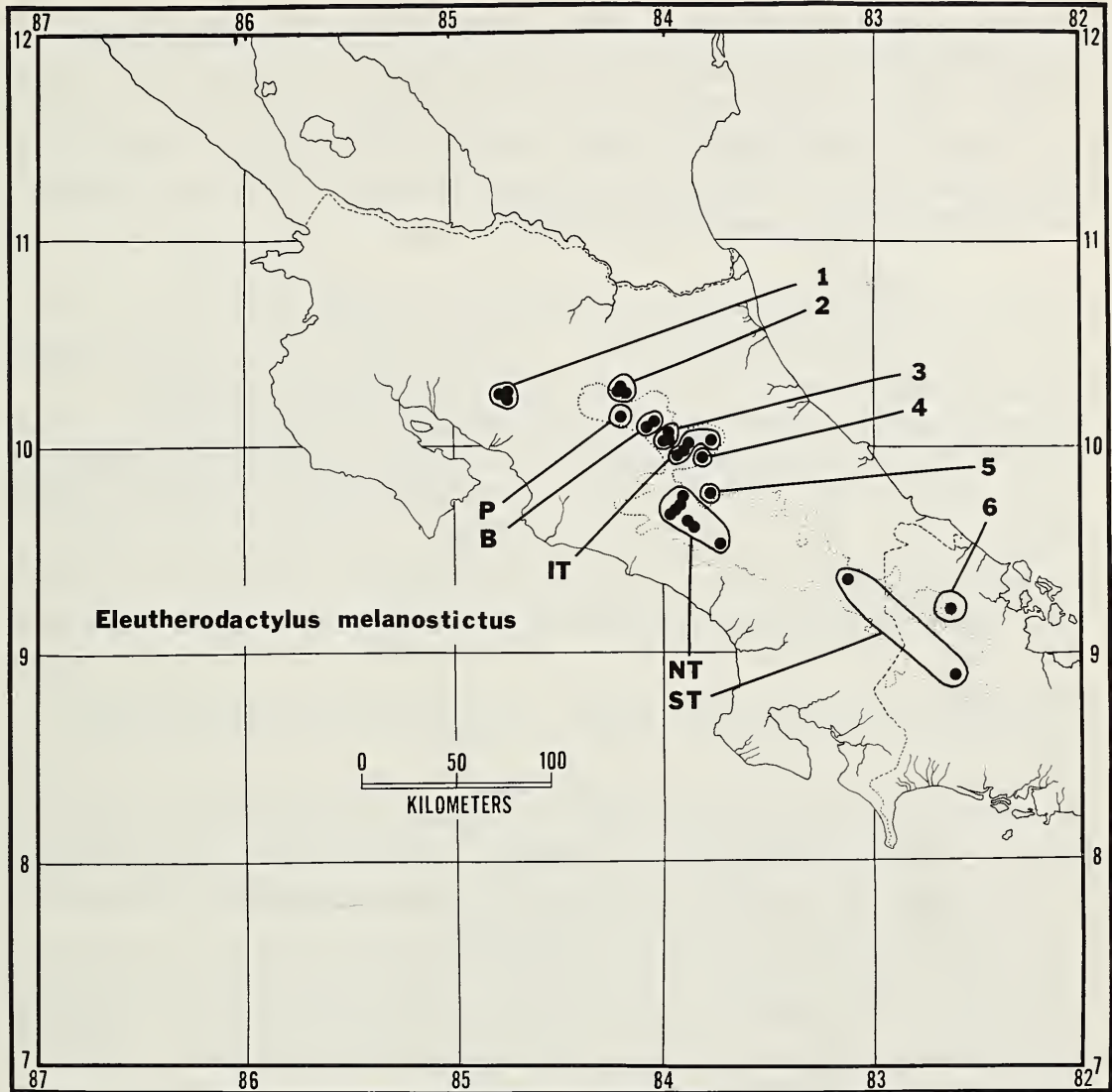


Fig. 1. Distribution of *Eleutherodactylus melanostictus* in Costa Rica and western Panama. Arabic numerals and letters indicate population samples discussed in text. The dotted line indicates the 1,500 m contour.

Monteverde de Puntarenas on the north to the slopes of Volcan Chiriqui to the south, between 1,150 and 2,483 m. Although these creatures are extremely similar to one another in most features of morphology, seemingly significant differences between montane (1,900–2,483 m) and slope (1,150–1,920 m) populations in coloration that correlated with minor morphological distinctions led us to regard them as separate species (Savage, 1976). As additional collections were made the supposed differences became less clear and we decided to undertake a sample by sample comparison to verify or refute our tentative conclusion.

The available material of this system has been grouped into a series of 11 populations (Fig. 1). Slope populations are designated by Arabic numerals,

montane populations by letters. The original comparisons (and greatest recorded differences) were made between the slope population (3) on the pass between volcanoes Barba and Irazu of the Cordillera Central of Costa Rica (La Palma–La Hondura pass) and the montane population (NT) on the Cordillera Talamanca along the Carreterra Interamericana in the same country. These differences are summarized below:

Population 3	Population NT
1. Snout obtuse, sloping in profile	1. Snout rounded in profile
2. Disk on finger II expanded, palmate; larger than tympanum	2. Disk on finger II barely expanded, round; smaller or equal to tympanum
3. Subarticular tubercles projecting	3. Subarticular tubercles flattened
4. Toe disks expanded, palmate, II–IV emarginate; largest at least as large as tympanum	4. Toe disks barely expanded, II–IV not emarginate; largest smaller than tympanum
5. Throat and venter usually light, with scattered punctations	5. Throat and venter dark, heavily pigmented
6. Light interspaces on posterior thigh surfaces yellow, yellow-green, purplish, or orange in life	6. Light interspaces on posterior thigh surfaces scarlet in life
7. Groin uniform or with two obscure light spots	7. Groin with well-developed dark bars

It seemed likely that if these differences were maintained with some consistency geographically and/or altitudinally, that two species were involved. For this reason we carefully compared all other populations for these features as follows from northwest to southeast.

1) Cordillera de Tilaran (1,500–1,580 m): snout round to obtuse, sloping; disk on finger II expanded; subarticular tubercles projecting; toe disks expanded; throat and venter light to dark; light thigh interspaces yellow to orange; groin not barred (N = 14).

P) Volcan Poas (2,100 m): snout rounded; disk on finger II small, round; subarticular tubercles flattened; toe disks small; throat and venter dark; thigh color not known; groin barred (N = 13).

2) East slope of Volcan Poas (1,200–1,590): snout round to obtuse, sloping or rounded; disk on finger II expanded; subarticular tubercles projecting; toe disks expanded; throat and venter light; light thigh interspaces yellow to magenta; groin not barred (N = 24).

B) Volcan Barba (1,828–1,920 m): snout round; disk on finger II small, round; subarticular tubercles intermediate; toe disks expanded; throat and venter dark; thigh color not known; groin barred (N = 5).

3) La Palma–La Hondura Pass (1,150–1,500 m): see summary above (N = 25).

IT) Volcanes Irazu and Turrialba (2,000–2,374 m): snout rounded; disk on finger II small; subarticular tubercles flattened; toe disks small; throat and venter dark; light thigh interspaces scarlet; groin uniform (N = 7).

4) South slope of Volcan Irazu (1,600 m): snout obtuse, sloping; disk on finger II expanded; subarticular tubercles projecting; toe disks expanded; throat and venter light; light thigh interspaces yellow, groin uniform (N = 2).

5) Tapanti (1,280–1,320 m): snout obtuse, sloping; disk on finger II expanded; subarticular tubercles projecting; toe disks expanded; venter intermediate in dark pigmentation; thigh color not known; groin not barred (N = 2).

NT) Northern Cordillera de Talamanca (1,900–2,482 m): see summary above (N = 7).

ST) Southern Cordillera de Talamanca (2,135–2,160 m): snout obtuse, sloping; disk on finger II rounded; subarticular tubercles flattened; toe disks expanded; venter intermediate in pigmentation; light thigh interspaces yellow; groin not barred (N = 2).

6) Slope of Cerro Pando (1,200 m): snout rounded; disk on finger II small, palmate; subarticular tubercles projecting; toe disks expanded; venter intermediate in pigmentation; thigh interspace color unknown; groin with a single bar (N = 1).

These comparisons indicate that montane populations from Volcan Poas (P), volcanes Irazu and Turrialba (IT), and the northern Talamanca region (NT) are essentially similar. Populations from the Cordillera de Tilaran (1) and the passes (2, 3) and slopes (4) of the Cordillera Central and northern Talamanca range (5) are almost identical to one another. Some overlap in snout profile and ventral coloration occurs between the three montane samples and the five populations from lower elevations. Nevertheless, it is possible to divide the material into two altitudinal groups based on these eight samples, a montane group from 2,000 m and above and a slope sample from 1,150 to 1,600 m, which differ principally in disk size, nature of the subarticular tubercles and presumably in posterior thigh color. Unfortunately these differences break down in the remaining population samples, one (B) from an intermediate elevation (1,828–1,920 m) on Volcan Barba and the others (ST, 6) from the southern portion of the Cordillera de Talamanca axis in Panama.

The Barba sample consists of three adult males (CRE 6463, 7094, 7130A) and a juvenile (CRE 7130B). In general coloration they agree with other montane examples in having dark venters and barred groins. Morphologically they further resemble montane members of the complex in having the disk on finger II round and small and the subarticular tubercles somewhat flattened, but not as much as in other montane populations. The toe disks, however, are somewhat larger than in other montane individuals and approach the size typical of slope populations.

The southern Talamanca sample consists of two examples, the holotype of *Lithodytes melanostictus* Cope and a single adult female from the vicinity of Cerro Punta, Provincia de Chiriqui, Panama (2,160 m). The female type

(USNM 30608) of *melanostictus* is now in very poor condition, so most characteristics cannot be determined. The Cerro Punta example agrees with montane samples in all characteristics except that the snout is obtuse in profile, the venter is not heavily pigmented, and the light thigh interspaces were yellow in life.

A single female (KU 114851) from the lower northern slope of Cerro Pando (1,200 m) also has a mixture of features. The finger disk size resembles those in montane samples, although larger. The shape of the finger and toe disks and the size of the latter approach those in other slope populations. The ventral coloration is intermediate.

Several possible interpretations may be made based on the available materials: 1) the Cordillera de Tilaran–Cordillera Central populations and the Cordillera de Talamanca samples represent two allopatric races or species; 2) the montane and slope populations represent related but distinct species differing only in the size of disks; or 3) only a single species is involved.

Alternative 1 does not seem valid, since the differences between montane and slope samples from each cordillera is greater than between the cordilleras and no feature will consistently separate available material into two geographic groups. Alternative 2 also seems contraindicated, since both montane and slope populations overlap to some extent in all characteristics except disk size and the Barba sample, from an intermediate elevation, is intermediate between the two groups in this feature.

Alternative 3 seems to be the only tenable conclusion based on this analysis. While montane and slope populations may be separated most of the time on the basis of disk size, subarticular tubercle profile, and coloration, we see no need to formally recognize altitudinal races within the complex. Many of the apparent differences may represent ecotypic influences associated with temperature related responses during development. Theoretically, at least, it is easier to conceive of the similarities among the isolated high elevation populations as the result of such influences rather than the result of fragmentation of a formerly continuous population. This idea implies that each montane isolate is more closely related to the adjacent slope population than to other montane members of the system. The single recognizable species including the eleven populations compared above is:

Eleutherodactylus melanostictus (Cope, 1875)

Fig. 2

Lithodytes melanostictus Cope, 1875:109, pl. 23, fig. 10.

Hylodes melanostictus.—Brocchi, 1881:56.—Günther, 1900:236.

Hylodes platyrhynchus Günther, 1900:230, pl. 67, fig. a (holotype: BM 1905-7-18,1/1947.2.15.81; Costa Rica).

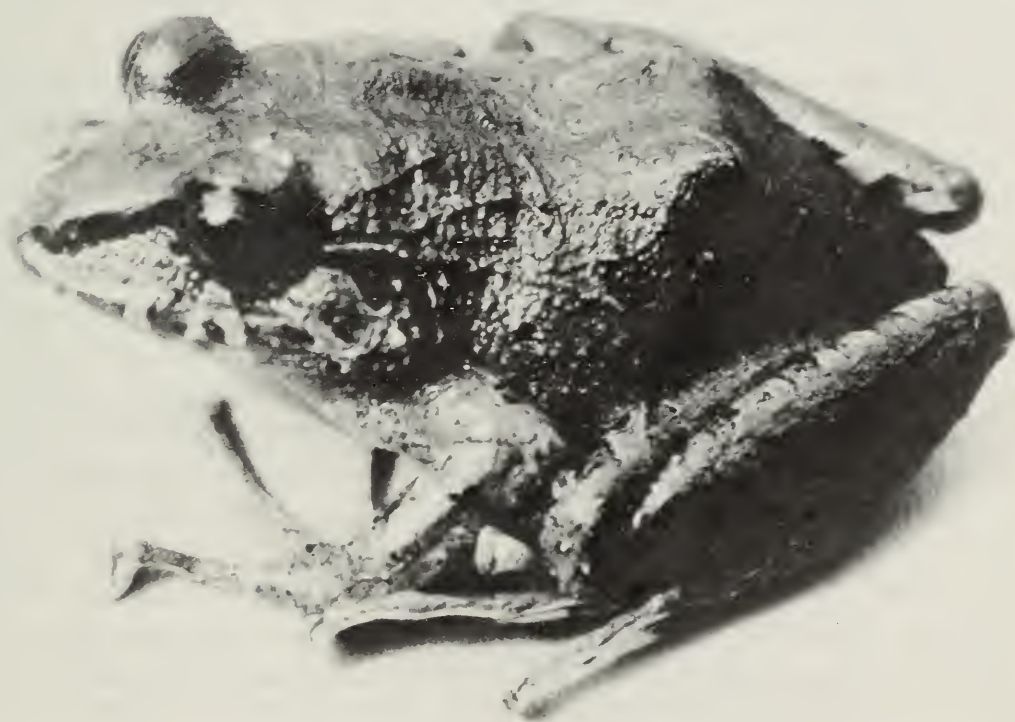


Fig. 2. *Eleutherodactylus melanostictus*: **upper**, male, CRE 7048-1, from 0.5 km W Bajo La Hondura, Provincia de San Jose, Costa Rica; **lower**, female, CRE 3895, from Monteverde, Provincia de Puntarenas, Costa Rica. Photographs courtesy of James L. Vial and James E. DeWeese.

Hylodes brocchi.—Günther (in part), 1900:236, pl. 68, figs. a–b.

Eleutherodactylus melanostictus.—Dunn, 1937:163.—Taylor, 1952:728.

Eleutherodactylus platyrhynchus.—Taylor, 1952:757, fig. 34.

Holotype.—USNM 30608, adult female, 50 mm in standard length; from Costa Rica, Provincia de Limon, Canton de Talamanca, Cerro Utyum, 2,135 m.

Diagnosis.—A moderate sized *Eleutherodactylus* (males to 43, females to 57 mm in standard length), immediately distinguished from all other species in lower Central America by having distinct dark thigh bars that continue down onto the posterior thigh surface. *E. melanostictus* belongs to a cluster of species placed in the *cruentus* group by Savage (1976) that have large finger and toe disks and a granulate venter and that lack both webbing and a tarsal fold.

The only two species within the group with which *melanostictus* might be confused, *E. cruentus* and *E. cerasinus*, have numerous accessory palmar tubercles on the hand and are much smaller in size (*cruentus* males to 25, females to 38 mm; *cerasinus* males to 23, females to 35 mm). The posterior thigh surface of *cruentus* is usually uniform dark brown to black, often with some clear yellow spots; the posterior thigh surface of *cerasinus* is almost uniform dull red in life (brown in preservative) with a very few small light spots in some examples.

Description.—Head outline from above subovoid to subelliptical; snout profile rounded to obtuse (sloping) in profile. Canthus rostralis sharp. Loreal area obtuse, slightly concave in section. Choanae small, ovoid, smaller than vomerine tooth patches; vomerine tooth patches transverse, posterior but internal to choanae, very narrowly separated on midline. Paired vocal slits and single internal vocal sac in males. Surfaces of head mostly smooth, with a single large supraorbital tubercle near posterior edge of upper eyelid, a series of weak superciliary tubercles along margin of upper eyelid and several smaller tubercles elsewhere on eyelid. Tympanum round in males, oval in females; internal, indistinct in both sexes, vertical diameter about $\frac{1}{2}$ length of orbit. A distinct supratympanic fold. Dorsum and upper limb surfaces relatively smooth with scattered tubercles. Finger I shorter than II; disk on finger I rounded. Disks well developed on fingers III–IV, at least 2 times width of digit, larger than tympanum, emarginate; disk on finger II slightly to definitely expanded, usually palmate. Whitish nuptial pad on thumb of adult males. Subarticular tubercles of fingers ovoid, flattened to slightly projecting, globular in profile; no supernumerary tubercles; thenar tubercle large, elongate; palmar tubercle large cordate, no accessory palmar tubercles. A distinct calcar. Toe disks smaller than finger disks, largest about equal to disk on finger II; disks on toes II–IV truncate to palmate, emarginate; disks on toes I and V very slightly expanded. No webbing. Subarticular tubercles under toes ovoid, slightly projecting and globular in

profile; no supernumerary tubercles; no plantar tubercles; inner metatarsal tubercle well developed, elongate, outer indistinct very small, round; no tarsal fold, but a very weak series of small outer tarsal tubercles may be present. A distinct small gland in groin; venter granulate.

Coloration.—Dorsal ground color pale tan to dark brown, in life brown, chestnut olive, olive-green or green; head uniform above or with distinct light (pink in life) enamel area on anterior surface of snout; dark brown to black interocular bar in most examples, sometimes bordered anteriorly by an obscure light area; usually a distinct dark canthal blotch extending from eye to nostril and involving upper loreal zone; a distinct black supratympanic stripe from eye to behind tympanum; tympanum covered by a dark spot; four distinct to obscure dark lip bars, the first continuous with the canthal blotch; two bars separated by a light area lie below eye. Iris golden in life, with a greenish cast. Five principal dorsal color patterns: i) essentially uniform with a few dark blotches and/or short lines on suprascapular and flank areas, sometimes with a definite W-shaped suprascapular dark mark; ii) with a broad mid-dorsal stripe, as broad or broad as interorbital area, contrasting in color with flanks and usually demarcated by an irregular narrow dark boundary; in life the center stripe is chestnut to reddish-brown; iii) with a narrow distinctly light (scarlet to yellow in life) mid-dorsal stripe, about half width of interorbital space, bordered by a black outline; stripe begins at interorbital or suprascapular region and continues to anus; iv) very narrow tan mid-dorsal stripe along median raphe, continuing as a narrow light longitudinal stripe on posterior thigh surface; and v) with distinct to obscure dark blotches and/or chevron-shaped marks dorsally. Flanks marked with a series of dark elongate oblique dark blotches, outlined by black, to give impression of a tiger pattern. Dark areas often flecked with metallic green, magenta or gold in life. Upper surfaces of forelimbs uniform to strongly barred with dark. Dorsal, anterior and posterior surfaces of thigh and calf marked with distinct dark bars; primary dark bars and light interspaces about same widths, although interspaces often split by a very narrow dark stripe; light interspaces on upper and anterior surfaces of thigh and calf suffused by darker pigment; on posterior thigh surface interspaces clear light and usually very distinct in most examples, although sometimes suffused with darker pigment; in life light areas on posterior surface are bright yellow, yellow-green, orange, salmon-pink, magenta, or scarlet. Throat and venter and undersides of limbs range from dirty white (in life and preservation) through intermediate stages to being heavily marked with dark pigment; in some examples dark pigment forms distinct dark spots. Groin area usually uniform like flank, sometimes with two obscure light spots or with elongate dark blotches similar to those on the flank in the tiger pattern phase. In life, light areas of groin and adjacent surfaces of venter and hindlimbs may be suffused with orange, pink, or red.

Table 1.—The centromeric indices (C.I.) and percent genome values (G) for the 11 pairs of chromosomes in the karyotype of *Eleutherodactylus melanostictus*.

Chromosome number	C.I.	G
1	1.37	16.9
2	1.47	13.4
3	4.07	12.1
4	2.04	11.9
5	1.15	9.8
6	1.26	8.8
7	1.28	7.0
8	7.00	6.6
9	7.00	5.1
10	7.00	4.6
11	7.00	3.7

Measurements.—In this section the notation gives the mean followed by the range in parentheses. Standard lengths (distance from snout to vent) are given in millimeters, other measurements as percentages of standard length. Values are based on samples of 10 adult males and 10 adult females randomly selected from montane and slope populations. The smallest juvenile available is 12 mm in standard length. Standard length, adult males 38.2 (35.0–42.6), adult females 43.8 (35.4–56.3); head length, males 38.0 (36.2–40.0), females 37.7 (34.0–39.5); head width, males 41.3 (38.4–45.6), females 40.9 (39.0–42.4); snout length, males 16.6 (15.0–18.3), females 16.9 (14.5–18.2); loreal length, males 11.1 (10.3–12.4), females 11.6 (9.0–13.0); length of orbit, males 16.2 (14.5–18.0), females 14.6 (12.8–17.2); height of tympanum, males 6.5 (5.0–7.9), females 6.1 (4.5–7.0); hindlimb length, males 199.1 (185.0–222.2), females 205.8 (168.0–225.2); tibia length, males 62.2 (54.1–76.4), females 62.3 (51.0–68.1). No marked sexual dimorphism is evident from these measurements, although the relative tympanum heights are slightly distinctive.

Karyotype.—Bogart (1970) described the karyotype of a specimen referred to this species from Monteverde, Costa Rica. We have karyologically examined one example (CRE 4130), a female, from near Cerro Punta, Panama, using the technique of Patton (1967) as modified by Lowe *et al.* (1966). 7 spreads were counted, 3 were photographed and the individual chromosomes were measured (Table 1).

The diploid number (2N) is 22 and the *nombre fundamental* (N.F.) is 36. The chromosomes form a gradually descending series with no obvious size groupings. Chromosome pairs (centromere placement according to the system of Levan *et al.*, 1964) 1, 2, 5, 6 and 7 are metacentric; 4 is submetacentric; 3 is subtelocentric; and 8–11 are acrocentric (Fig. 3).

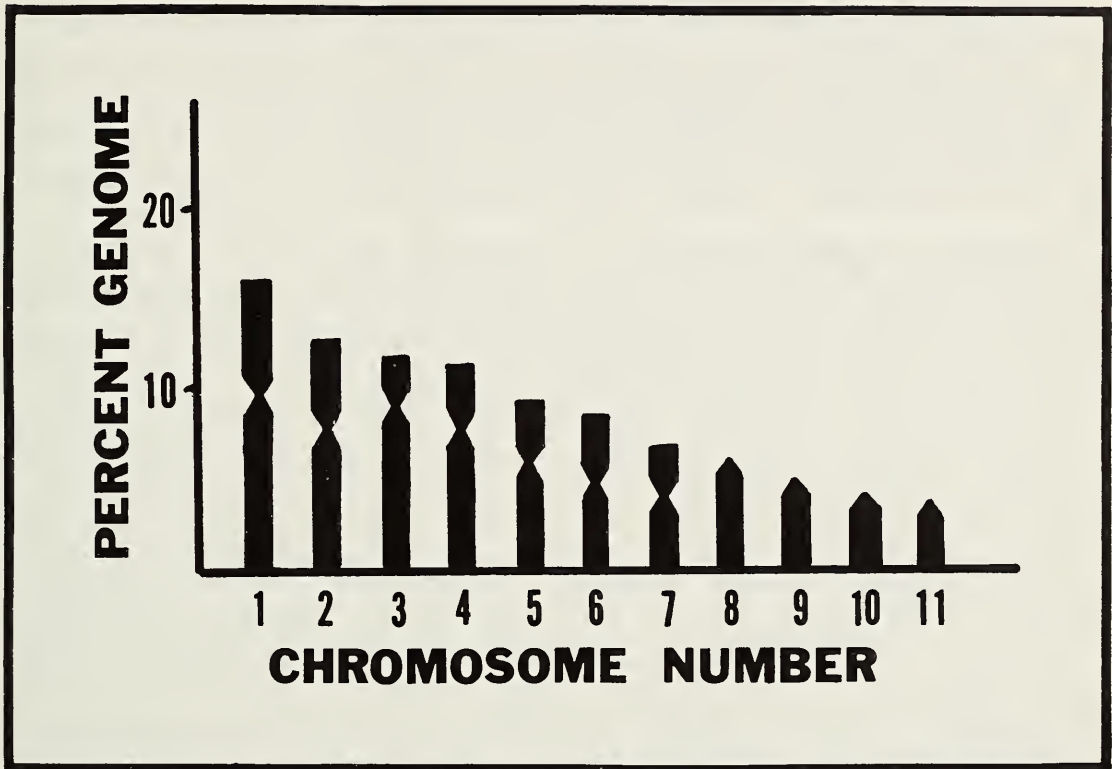


Fig. 3. A representative idiogram for *Eleutherodactylus melanostictus*.

Bogart's (1970) description and figure differ slightly from our data, with $2N = 22$ and $N.F. = 38$. Chromosome pairs are 1, 5, 6 and 8 metacentric; 3 and 4 submetacentric; 2 and 11 subtelocentric; and 7, 9 and 10 acrocentric, according to Bogart. Essentially his interpretation is that there is one less acrocentric and one more subtelocentric pair, one less metacentric and one more submetacentric and that 11 is subtelocentric rather than acrocentric. This latter interpretation or observation explains the difference in $N.F.$ between Bogart's example and our data. These apparent differences may be due to 1) differing techniques of preparation and measurement of the spreads; 2) variation, either individual or populational; or 3) misidentification of the Monteverde specimen by Bogart. Although we have been unable to locate Bogart's voucher specimen to confirm the identification, *E. melanostictus* is so distinctive in color pattern that the last alternative seems unlikely. Until additional karyological preparations are available, no decision between the other two alternative explanations is possible.

Jaw musculature.—The depressor mandibulae has a single slip originating on the dorsal fascia with a few fibers coming from the squamosal (dfsq). The adductor mandibulae externus superficialis is present (e). The jaw muscle formula $dfsq + e$, follows the terminology of Starrett (1968).

Ecological notes.—Taylor (1952:761) reported the collection of a number

of examples of this form from bromeliads, where they may hide during the day. Most specimens in our samples (La Palma, La Hondura and Monteverde) are males taken at night while calling from herbaceous vegetation 1.0–2.5 m above the ground in dense rainforest habitats. USC examples from the Talamanca range are mostly males found under rocks or logs during the day.

Distribution.—Evergreen forests of the upper portion of the premontane and lower montane zones on both Atlantic and Pacific slopes of the Cordilleras de Tilaran, Central, and Talamanca of Costa Rica and the extension of the latter as the Chiriqui massif of western Panama, 1,128–2,483 m (Fig. 1).

Locality records.—COSTA RICA: no other data; ALAJUELA: Isla Bonita; Hda. Cayuga; Cinchona; above Cinchona (1,590 m); E slope Volcan Poas (1,590 m) 1 km W Poasito, Rio Poasito; CARTAGO: 1.6 km NE Casa Mata; 2.5 km W Sanatorio Duran, Volcan Irazu; El Empalme and 16 km S; 2 km NW Pastora, Volcan Turrialba; Volcan Irazu (2,000 m); Rio Quiri, Tapanti; nr. El Sesteo; 1–2 km SE Santa Teresa; Trinidad; CARTAGO–SAN JOSE: 1 km S El Empalme; Cerro de la Muerte; HEREDIA: Volcan Barba (1,828 m); Cerro Chompipe; LIMON: Cerro Utyum (2,135 m); PUNTARENAS: 1.75, 2.6 km ESE, 1.25, 2.25 km SE and Monteverde; SAN JOSE: Boquete Camp; La Hondura; 0.5 km W Bajo La Hondura; 2 km E Las Nubes; 0.5 km E, N, S and La Palma; 1.4 km S Alto La Palma; 3 km SE and Rancho Redondo. PANAMA: BOCAS DEL TORO: N slope Cerro Pando (1,200 m); CHIRIQUI: 2 km W and 0.5 km N Cerro Punta.

Remarks.—We have examined holotypes of both *Lithodytes melanostictus* and *Hylodes platyrhynchus*. The former (USNM 30608) is now in very poor condition and some of the features noted when it was examined 14 years ago by Savage are no longer distinguishable. The distinctively barred thighs are still apparent and all other characteristics and the original description (Cope, 1875) confirm its identity with the montane populations of the Cordillera Talamanca–Chiriqui axis of Costa Rica and Panama.

Günther (1900:226, 236) ascribed a smooth ungranulated venter to this specimen, doubtless based on Cope's (1875:109) statement "skin everywhere smooth." Cope probably was referring to the upper surfaces of the body. However, the rugosely granulate venter of this and many other *Eleutherodactylus* is distorted in poorly fixed specimens or those long in preservative.

The type of *Hylodes platyrhynchus* (BM 1905-7-18,1/1947.2.15.81) remains in excellent condition. It is an adult female 57 mm in standard length and morphologically agrees in all ways with the sample (3) from the pass between Volcanes Barba and Irazu. The dorsal color pattern is of type i) described above. The head markings and thigh barring as illustrated by Günther (1900, pl. 67A) confirm the identification.

The most consistent and distinctive characteristic of *E. melanostictus* is the continuation of the dark thigh bars onto the posterior surface of the thighs. Since the light interspaces between the dark bars are usually brightly colored in life, the contrasting dark versus brilliant yellow, yellow-green, orange, magenta, or red makes this species readily recognizable in the field. Two examples here referred to this species exhibit a considerable reduction and suffusion of the light interspaces with dark pigment to obscure the usually contrasting pattern. An adult male (CRE 3296), 37 mm in standard length, from near Bajo La Hondura, Costa Rica, has the light interspaces reduced to several small light spots while the margins of the dark bars are obscured by the suffusion of dark pigment. On close inspection the typical dark thigh bars may be observed. This example also has the throat, venter and undersides of limbs heavily covered with dark pigment, a condition unusual in other examples of *E. melanostictus* from this locality. As a matter of fact it has the greatest degree of ventral dark pigmentation within all samples of this species. In all other features this frog agrees with our concept of the species and we conclude that it is a variant with much more extensive development of melanin than is usual.

A second extremely dark example of this form is an adult female (CRE 3985), 56 mm in standard length, from Monteverde, Costa Rica. In all features but coloration this example is a typical *E. melanostictus*. Essentially, the Monteverde frog has a very dark dorsum and extensive dark pigmentation over all the under surfaces. The light interspaces on the thigh surfaces are very heavily suffused with dark so that the dark thigh bars appear outlined by a very narrow light line. The extensive dark suffusion makes the dark bars obscure on the posterior thigh surface, since even the bordering remnant of the interspaces is lost as the bar proceeds downwards. The bars are barely distinct from the heavily suffused interspaces in this region, but can be distinguished by their heavier concentration of black pigment.

Relationships

Evaluation of evolutionary relationships among the multitudinous species of *Eleutherodactylus* has long defied the capabilities of herpetologists. Most attempts to group clusters of the 400 or so nominal species now placed in the genus have been based primarily on external "key" characteristics of dubious aid in discerning all but the most closely related species similarities. Recently Savage (1976) and Lynch (1976) have applied two somewhat different approaches to establishing divisions within *Eleutherodactylus*. The former recognized species groups comprised of species that are extremely similar morphologically and are probably evolutionarily closely allied. Lynch follows a second alternative of forming groups that correspond to sub-genera, without giving them formal nomenclatural status. Both methods

have thus far proven inadequate to cope with the complex mosaic of superficial morphological characteristics that have been combined over and over again in distantly related species of *Eleutherodactylus* for the reasons already pointed out by us (Savage and DeWeese, 1979).

The, for the most part, unpublished studies on jaw musculature (Starrett, 1968), serum proteins (Harris, 1973) and karyology (DeWeese, 1976) of *Eleutherodactylus* suggest that at least six major evolutionary lineages are recognizable within the limits of the genus (*sensu lato*). In most cases these lineages do not conform to the groupings recognized by Lynch (1976) based on external and skeletal morphology. That the problem is real is suggested by the fact that Savage (1976) included *E. melanostictus* in the *melanostictus* group, its synonym *platyrhynchus* in the *cruentus* group; Lynch (1976) regarded the latter taxon as belonging to his *unistrigatus* group in which he included *cruentus* and its allies.

Eleutherodactylus melanostictus morphologically, but apparently only superficially, resembles the members of the *cruentus* group (Savage, 1976) in having a strongly granulate venter, large digital disks, and no toe webbing or tarsal fold. Other Central American species included in this group by Savage are: *altae*, *pardalis*, *cruentus*, *cerasinus*, *ridens*, *frater*, *caryophal-laeeus*, *moro* and *monnichorum*. Studies by DeWeese (1976) on the karyology of most of these forms and the less extensive serum protein data of Harris (1973) indicate that the *cruentus* group is a composite of species from rather diverse origins that happen to share a series of trivial morphologic features in common. Lynch (1976) included all of these disparate forms among the 92 species placed in his *unistrigatus* group.

In terms of jaw muscle features, *E. melanostictus* shows the greatest similarity to the *fitzingeri* and *rugulosus* groups of Savage (1975, 1976), which are included together in the *fitzingeri* group of Lynch (1976). As pointed out by Starrett (1968) the most consistent and evolutionarily significant of these muscles is the condition of the adductor mandibulae. Three conditions may be recognized: 1) both an adductor mandibulae posterior subexternus and an externus superficialis present (s + e); 2) only the posterior subexternus present (s); or 3) only the externus superficialis present (e). *Eleutherodactylus melanostictus*, like the members of the *fitzingeri-rugulosus* groups now examined from Central America, has the e condition. All known members of the *unistrigatus* group of Lynch (1976) have the s condition.

In addition, the features of the depressor mandibulae of *E. melanostictus* support a similar relationship. Starrett (1968) recognized 10 patterns of depressor mandibulae muscle origins. Six of these conditions occur within the family Leptodactylidae and four are known to occur in *Eleutherodactylus*. These conditions are: 1) a single slip principally from the dorsal fascia, but with a few fibers from the squamosal (dfsq); 2) a single slip principally from the dorsal fascia, but with a few fibers from the squamosal and annulus

tympanicus (dfsqat); 3) three slips, one each from fascia, squamosal and annulus tympanicus (DFSQAT); and 4) three slips, with superficial slip from fascia and annulus tympanicus and a deep slip (internal to the others) from the squamosal (DFSQ_dAT). We regard conditions 1 and 2 as representing only slight variation in a single character.

The depressor mandibulae in *E. melanostictus* are of condition 1 (dfsq). This condition is typical of the *fitzingeri-rugulosus* groups of Savage (1976). Some species in this complex (*brocchi* and *rugulosus*) have condition 2 (dfsqat). All members of the *unistrigatus* group of Lynch (1976) for which this character is known have condition 4 (DFSQ_dAT).

Karyologically, *E. melanostictus* agrees in diploid number ($2N = 22$) and N.F. (36) with *E. talamancae* of Costa Rica and Panama, *E. berkenbuschii* (recently revived by Savage and DeWeese, 1979) and *E. vocalis* of Mexico, and *E. rayo* of Costa Rica, all members of the *fitzingeri-rugulosus* complex. Other leptodactylids with the same numbers are *E. decoratus* (*alfredi* group) and *Hylactophryne augusti* (of Mexico); and *Leptodactylus podicipinus*, and *L. wagneri* of South America. Of these species the chromosome features of *E. melanostictus* most closely approach those of *E. berkenbuschii*. Members of the *cruentus* group of Savage (1976) and the *unistrigatus* group of Lynch (1976) for which the karyology is known have $2N = 26, 32, 34$ and N.F. = 32, 36, 46 (Bogart, 1970; DeWeese, 1976).

What a dilemma! A frog that in external and skeletal morphology clearly belongs with one major section of the genus (the *unistrigatus-cruentus* stock), but in extremely important features of jaw musculature and karyology belongs elsewhere (*fitzingeri-rugulosus* complex)! Obviously our knowledge of this marvelously complex and perverse genus is far from complete. It may be that *E. melanostictus* represents a primitive stock ancestral to the two very distinctive major groups (*unistrigatus-cruentus* and *fitzingeri-rugulosus*). Full investigation of this possibility awaits more extensive data on jaw musculature and karyology. Until these studies are completed it seems wise to retain *melanostictus* in a distinct monotypic group.

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